WATER BALANCE IN ANOMURAN LAND CRABS ON A DRY ATOLL

WARREN J. GROSS

Division of Life Sciences, University of California, Riverside, California

Degrees of the terrestrial habit have been achieved by many representatives of the decapod Crustacea. Still, none are completely successful, for they are all bound to water by their reproductive habits. Some of the most successful invaders of land in this group are anomuran crabs, which despite their abundance and common occurrence in tropical regions have received little attention with respect to the physiological adaptations, especially those concerned with water regulation, which make life on land possible for them. Edney (1960) reviews the subject of terrestrial adaptations among the Crustacea. Gross (1955) demonstrated in laboratory experiments that the anomuran cocoanut crab, *Birgus latro,* can control its blood concentration by selecting water of appropriate salinity, and when given a choice it will visit fresh water more often than sea water. Gross and Holland (1960), on the other hand, demonstrated a similar behavioral mechanism in the hermit crab, *Coenobita perlatus,* but this species showed a definite preference for sea water over fresh water when offered a choice.

The above mentioned investigators also demonstrated tolerance to a wide range of blood osmotic concentrations in *Birgus* and *Coenobita.* Yet no information is available concerning the range of variation experienced by these crabs in their natural environments. On the other hand, Harms (1932) made a few freezing point determinations on the blood of *Birgus* and Pearse (1934) did the same on *Coenobita clypeatus,* but these workers were not explicit as to the environmental conditions under which the blood samples were taken from the animals.

The field studies of present investigation were conducted at the Eniwetok Marine Biological Laboratory at Eniwetok Atoll, Marshall Islands, during the months of February and March of 1963. This is typically the dry season of the year, each of these two months having a normal precipitation of less than 1.9 inches whereas the normal annual rainfall is about 50 inches (Arnow, 1954). This time of the year, then, would usually be a critical period for land crabs which depend on water sources other than the sea, but the particular period during which this study was conducted was even more critical than usual because the February precipitation was only 0.19 inch and throughout March, up to the 27th when field studies were terminated, the precipitation was only 0.28 inch.

This study reveals the range of blood concentrations endured by three species of terrestrial anomuran crabs during a drought and furnishes information concerning their sources of water under the stressed conditions of the dry season. Eniwetok Atoll is especially suitable for this study because its islets present different extremes in environment from well wooded conditions, rich in detritus, to exposed conditions of poor vegetation and dry soil consisting mostly of coral sand.

Materials and Methods

Three anomuran crabs of the family Coenobitidae were studied in the field and in the laboratory: The cocoanut crab *Birgus latro* Linnaeus, and the hermit crabs, *Coenobita perlatus* Milne-Edwards and *Coenobita brevimanus* (Dana).

All three species were studied in the laboratory at Eniwetok under conditions which are described below. However, a group of *Coenobita brevimanus* was flown to Riverside where it was maintained for several weeks in cages in a greenhouse where the temperatures varied between 20° and 33° C. Here the animals had a choice of sea water or fresh water made available in open dishes or dispensers which permitted estimation of the volume of water used. Also available was a box filled with a mixture of peat moss and sand, which was maintained in a damp condition with fresh water. This was to simulate the damp detritus of cocoanut piles where this species was captured. Cocoanut and fish meal were made available for food. Thus, the laboratory conditions under which *C. brevimanus* was maintained in Riverside are believed to approximate those it encounters in nature with respect to water relations, and hereafter shall be referred to as "normal." All animals used in this investigation were mature and between molts. The smallest specimens of hermit crab weighed approximately 20 g. without the shell. The carapace width of *Birgus* ranged between 4.5 cm. and 15.0 cm. Sexes were equally divided for *Birgus*. However, note could not be made of sex for most *Coenobita* in the field because of the difficulty in removing the crabs from their shells. On the basis of a token sampling, the sexes seemed about equally divided for both species of *Coenobita*.

Blood was extracted in the field from all three species by puncturing the arthrodial membranes at the joints of the appendages by means of glass pipettes. The blood was introduced into vials which in turn were placed into a Thermos bottle filled with ice held in a plastic bag to prevent water from leaking into the screw-cap vials. Such samples remained cold until returned to the laboratory at Eniwetok for analysis.

Urine was extracted only in the laboratory because this required immersion in cold water to relax the animal, a treatment from which it readily recovered. Care was taken to dry the nephropores before inserting the cannula.

Osmotic concentrations of body fluids were determined by means of a Mechrolab vapor pressure osmometer. In the case of blood this required the removal of the clot to prevent coagulum from adhering to the thermistor of the osmometer. One reading by means of the above osmometer on uncoagulated whole blood of *C. brevimanus* gave the same value as the serum of the same sample within the precision of measurement of the instrument, which has less than a 2% error with the methods used in this investigation. Also, Prosser *et al.* (1955) and Gross (1963a) have demonstrated no osmotic difference between blood and serum of *Pachygrapsus* and *Hemigrapsus*, respectively. There is good reason, therefore, to assume no difference between the osmotic concentration of blood and serum for all species examined in this study.

Salinities of water (both surface water and crab shell water) were estimated in the field by means of an American Optical Company TS meter (Goldberg refractometer). This instrument can be carried conveniently in the pocket and is self-correcting for temperatures between 15° and 37° C. The error was less than

3% in the range of normal sea water (3.43% salt). This standard for normal sea water is a common salinity in the coastal waters near Riverside. However, sea water from the open lagoon at Eniwetok was observed to be 104% of the above standard.

Results

Both *Birgus* and *C. brevimanus* were found only in secluded, protected situations. In all cases *C. brevimanus* was found in areas of heavy vegetation, burrowed in piles of rotten cocoanuts often associated with *Birgus*. This hermit crab was never found in or near the sea. *Birgus*, with the exception of those specimens found on Jieroru Islet (to be discussed below), also was observed to be confined to densely vegetated areas near or in piles of rotten cocoanuts. The piles of cocoanuts are rich in detritus. In their depths they were damp to the touch despite the recent paucity of rain. *Coenobita perlatus* is by far the most common of the three subjects at Eniwetok. It is commonly found in exposed situations close to the edge of the sea, where it aggregates in large numbers during the day among the roots of trees and shrubs (*Messerschmiddia* and *Scaevola*). Young specimens of *C. perlatus* were found on islets completely devoid of vegetation, usually aggregated in the daytime under wreckage or debris. However, this species was commonly observed in the forested areas, particularly at night when it was most active. It occasionally was found burrowed in piles of rotten cocoanuts along with *Birgus* and *C. brevimanus*, but this was not common. *C. perlatus* was observed to enter brackish water of pools and sea water of the lagoon. It is of interest that the largest aggregation of this species found was at the edge of a pool of brackish water (58% sea water) which was in a compartment of a wrecked barge. During this study the only standing fresh water observed was shortly after a rain squall, in the form of droplets on leaves. This was short-lived and was observed only once, although during the two-month drought period local rain squalls of short duration were common throughout the atoll.

Figure 1 illustrates the serum osmotic concentrations of the three species collected from different environmental situations. The blood samples for *Birgus* and *C. brevimanus* from the cocoanut piles were taken on Igurin and Giriinien Islets during the day, and samples from the two sites for both species were not significantly different from each other. However, the mean concentration for *Birgus*, 74.7% sea water (Fig. 1, A), was significantly less than the mean value for *C. brevimanus*, 80.3% sea water (Fig. 1, C), $P < 0.01$. The value for *Birgus* compares closely with that given by Harms (1932) although the conditions in which the animals were found or kept are not described explicitly by this worker. On the other hand, the sera of three specimens of *Birgus* collected in the daytime from deep dry burrows on Jieroru Islet were 88.4, 91.2 and 95.2% sea water (Fig. 1, B). This islet is relatively bare of vegetation; all palm trees have been destroyed and detritus is scarce. The crab burrows, which were deep and well sealed in two cases, were dug in a substrate which was dusty and dry to the touch. The only apparent source of water was the lagoon. All three crabs were active and seemed to be in excellent condition.

As mentioned above, *C. brevimanus* was found only in cocoanut piles where the substrate was damp. It was not observed foraging at night, as were the other two species, but such activity was probably overlooked because of the relatively small population of *C. brevimanus*. Blood samples were taken from the cocoanut crabs only in the daytime when they probably had been removed from any source of surface water for hours. The values for blood concentration in this species (Fig. 1) are thus believed to be maximum.

Coenobita perlatus, however, was found in a variety of environmental situations which is reflected in the wide range of serum osmotic concentrations. Figure 1 reveals the mean serum concentrations for the following environments: exposed and inactive close to lagoon's edge in daytime, 124% sea water (Fig. 1, D); filling shells with lagoon water at night, 128% sea water (Fig. 1, E); active in wooded area at night, 128% sea water (Fig. 1, F); filling shells with brackish water at night, 115% sea water (Fig. 1, G); inactive and burrowed in piles of rotten cocoanuts in daytime, 106% sea water (Fig. 1, H). It should be pointed out that in both

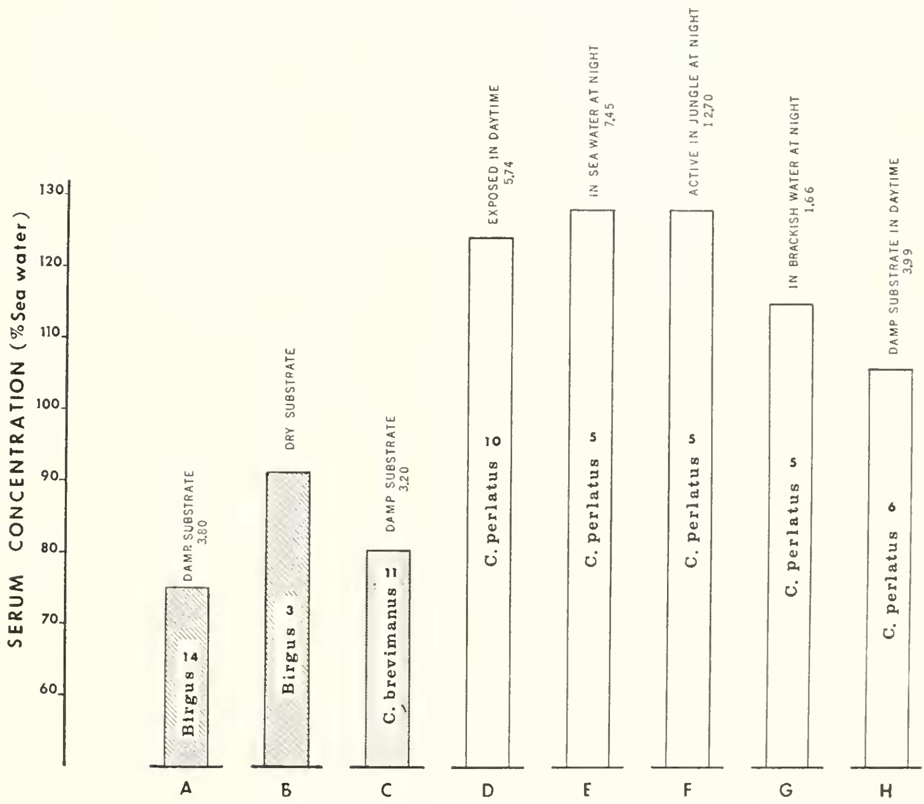

FIGURE 1. Osmotic concentration of serum sampled in different field conditions from terrestrial crabs. Height of bar represents mean serum concentration. Numeral inside bar indicates number of cases. Numeral above bar represents standard deviation of the mean. All three values for the Jieroru *Birgus* (B) are given in text. Brief descriptions of environments are indicated over bars. Details of conditions are given in the text.

groups which were filling their shells (E and G, Fig. 1), about one-half hour was allowed to lapse after capture before blood samples were taken. This was to permit any possible equilibrium to take place between shell water and blood following the filling process. The lowest blood concentration observed for this species was 102% sea water from a crab taken in a pile of cocoanuts; the highest observed was 150% sea water from an active crab which was foraging in the wooded area at night. Thus, *C. perlatus* maintains its blood concentration considerably higher than *Birgus* or *C. brevimanus*, even when found in similar environments where the availability of water for all three species is the same (*e.g.*, wooded areas and burrowed in cocoanut piles). On the other hand, *C. perlatus* does not maintain such uniform serum concentrations as the other two species when it has equal opportunities with respect to the availability of water.

When *C. perlatus* was exposed exclusively to sea water for more than two weeks in the laboratory, the concentration of its blood, as calculated from total cations,

TABLE I

Shell water concentrations in Coenobita captured in the field

Species	Collecting site and conditions	Concentration of nearest observed surface water (% sea water)	No. cases	Mean shell water concentration* (% sea water)
C. perlatus	Japtan Islet; edge of lagoon under board	104	6	125 (119–140)
	Igurin Islet near sump under board	76	3	105 (104–106)
	Igurin Islet in compartment of wrecked barge high on beach of lagoon	58	5	97 (87–111)
	Igurin Islet; active in wooded area	104	5	125 (117–134)
	Igurin Islet in water at edge of lagoon	104	5	107 (104–108)
	Jieroru Islet; inactive under roots of trees at edge of lagoon	104	7	126 (109–131)
	Giriinien Islet from piles of cocoanuts	104	3	115 (105–134)
C. brevimanus	Giriinien Islet from piles of cocoanuts	104	5	80 (73– 87)

* Values in parentheses indicate observed range.

averaged less than 110% sea water (Gross and Holland, 1960). The higher values observed in the field, therefore, suggest that significant evaporation takes place during prolonged absence from a source of water in the field.

In all observed field cases both *Birgus* and *C. brevimanus* maintain their serum concentrations below the concentration of the nearby sea; even *Birgus* from Jieroru was thus.

No obvious trends in the serum concentration were observed with respect to sex or size in any of the species examined.

The concentration of water carried in the shells of the hermit crabs was measured in the field in order to reveal something about the sources of water for these crabs in nature. Table I presents the observed concentration for shell water taken from the two species of *Coenobita* from different environmental conditions. It should be pointed out that in many cases water could not be taken from the crab's adopted shell. For example, only 5 out of 21 specimens of *C. perlatus* from the wooded area yielded water. This might be expected because of the relatively great distance to the sea. The salinity of the shell water, unless recently filled, was higher than the sea and was close to the concentration of the animal's blood. Thus, the mean ratio, shell water concentration/serum concentration, for five cases of *C. perlatus* from which both samples were taken was 1.04; range: 1.02–1.09. Obviously this ratio would be different in a crab which was in the process of filling its shell. As mentioned above, this species was observed filling its shell at night, both with sea water at the edge of the lagoon and with brackish water from a pool. It is interesting that shell water from all crabs captured in the morning, close to the lagoon's edge (Jieroru Islet), was highly concentrated. This suggests that an osmotic equilibrium was established between shell water and blood because there had been little opportunity for evaporation of the shell water which probably had come from the sea only a few hours earlier.

TABLE II

Shell water and serum concentration of Coenobita brevimanus maintained in the laboratory under different conditions

Condition	Period of exposure (days)	Mean shell water concentration (% sea water)*	No. cases	Mean serum concentration (% sea water)	No. cases	S. D.
I						
F.W., S.W. and damp peat moss "normal"	21	76.4 (67.0–84.6)	5	79.7	5	1.45
	>28	74.2 (64.2–104)	7	—	—	—
II						
S.W. only and damp peat moss	2	95.3 (87.5–99.2)	3	—	—	—
	5	85.8 (64.2–104)	4	95.6	5	7.16
	>15	115 (102–131)	5	—	—	—
III						
Damp peat moss only	>15	no water		86.4	6	10.2

* Values in parentheses indicate observed range.
F.W. = fresh water, S.W. = sea water.

The shell water of *C. brevimanus*, on the other hand, was dilute to the sea in all five field cases observed (Table I). Still, no source of surface brackish water or fresh water could be found within several hundred meters of the collecting area. Again, however, the concentration of shell water was close to isotonicity with the blood of *C. brevimanus*. Large quantities of shell water are commonly found in *C. brevimanus*. Unfortunately, when the largest aggregation of this relatively uncommon species was found (on Japtan Islet), there was no available means of measuring the salinity of the shell water. Again, however, the only visible source of surface water was the sea which was at least 200 meters away.

Now there is no doubt that *C. perlatus* fills its shell with available surface water (Table I); however, no such process was observed for *C. brevimanus*. With the relative scarcity of this species on the islets studied, however, such a process easily could have been overlooked. Table II presents the results of experiments performed in the laboratory at Riverside, to determine the source of shell water in *C. brevi-*

manus. Thus, in Group I, which was given access to surface sea water, fresh water and peat moss dampened with fresh water, the shell water averaged about 75% sea water; after three weeks in such a situation the osmotic concentration of the blood averaged 79.7% sea water, as compared to the average 80.3% sea water for *C. brevimanus* sampled in the field. It thus seems that the laboratory condition termed "normal" in this investigation does indeed approximate field conditions.

Group II, on the other hand, which was presented only free sea water and damp peat moss, showed low concentrations for shell water for at least 5 days after transfer from "normal" conditions. However, after 15 days' exposure to this condition, the salinity of the shell water in every observed case was higher than the available normal sea water. The low concentration of shell water during the early part of this experiment, then, must have been a residue from the previous "normal" condition where fresh water was present, and/or a matter of dilution of the normal sea water taken into the shell by the water from a hypotonic blood which diffused outward through the body wall. Also, it will be noticed (Table II) that the blood osmotic concentration for this group averaged close to that of the available free sea water (95.6% sea water). The lowest value in this experimental group (87.6% sea water) was higher than the highest value observed for any field sample (85.2% sea water). All animals were in apparently good condition at the end of this experiment, thus indicating tolerance to elevated blood concentration. There is evidence, then, that *C. brevimanus* will use sea water to fill its shell when fresh water is not available. It follows, however, that the low osmotic concentration of shell water and serum observed in the field samples is not the result of diluting sea water with fresh water which is absorbed from the substrate.

Animals of Group III remained viable for more than two weeks in the absence of any surface water. These persistently burrowed in the damp detritus which they introduced into their shells; they fed, and were active at the termination of the experiment. However, shell water could not be obtained from this group. Thus, it does not seem likely that the large quantities of shell water observed in this species in the field could have been absorbed from the damp substrate and then secreted into the adopted shell. While the serum concentration of this group averaged 86.4% sea water, which was somewhat higher than the field samples as well as the laboratory crabs from the "normal" condition (Group I, Table II), the range was 74.8–104% sea water. This is a higher maximum and a lower minimum than observed for the field samples (74.9 and 85.2, respectively).

It was observed following this treatment that these crabs completely drained two watering devices in less than 15 hours, one containing about 500 ml. of fresh water, the other about 200 ml. of sea water. Such quantities obviously could not be consumed internally by six crabs. Rather it was taken into the shell repeatedly and spilled outside of the watering troughs. Six animals maintained in the "normal" condition consumed less than 100 ml. of fresh water daily and only traces of sea water. Such a behavior suggests that the crabs had become dehydrated in the absence of free surface water, but since the blood concentrations remained relatively low, it also suggests that salts were lost by the crab to the damp substrate. It is apparent, nevertheless, that *C. brevimanus* could survive, burrowed in rotten cocoanut piles without access to fresh water during an extended drought such as is common at Eniwetok.

Similarly, when crabs of Group II were given a choice of fresh water or sea water after having been deprived of fresh water for more than two weeks, they drained the fresh-water dispenser of about 500 ml. in a period of four hours. No loss of sea water could be detected from its respective dispenser. After a period of 15 hours 800 ml. of fresh water had been used, even though the position had been exchanged with sea water, and although there were indications that the crabs had visited sea water, no detectable amount had been used. These experiments strongly suggest a decided preference for fresh water by this species and further suggest a behavioral mechanism for maintaining proper water balance such as that described for *Birgus* by Gross (1955) and for *Coenobita perlatus* by Gross and Holland (1960).

Hydration and dehydration in hermit crabs could not be measured by weight changes because forceful removal of the animal from its adopted shell caused loss of fluid which could not be measured with precision. Measurement of weight changes of the animal in its gastropod shell were of no value because, as mentioned above, undetermined amounts of solid material were habitually introduced into the shell by the animal.

Figures 2 and 3 illustrate the results of experiments conducted in the laboratory at Eniwetok concerning the effects of available fresh water or sea water on the serum osmotic concentration of *C. brevimanus* and *Birgus* in a situation where they could not burrow but where they could readily reach water in an open dish, as well as a supply of fresh cocoanut. Thus, 9 days following transfer from a condition where both fresh water and sea water were available to where only fresh water was present, the serum concentration of *C. brevimanus* was slightly higher on the average than the mean of the field samples; after 17 days the serum concentration was slightly lower than the field samples (Fig. 2). But 5 days after fresh water was replaced with sea water, the blood concentration rose dramatically, all five cases being far higher than anything observed in the field.

A similar phenomenon was observed on two specimens of *Birgus*. It will be noted in Figure 3 that the serum of one specimen rose in concentration considerably above its field value, even after it was exposed exclusively to fresh water for more than two weeks. This possibly was caused by the crab's inability to burrow, thus permitting water loss from the body surface through evaporation. The second specimen also demonstrated a slight increase in its blood concentration and while it, too, was unable to burrow into a damp substrate, it was the larger specimen of the two which may have allowed it greater physiological stability in the above captive condition. Nevertheless, both specimens, when exposed exclusively to normal sea water for five days, demonstrated increases in the serum concentration to levels which were matched only by crabs sampled in the dry situation on Jieroru Islet. Therefore, when only sea water is available, *Birgus* is unable to maintain the low blood concentrations observed in the field on Igurin and Giriinien Islets. Also, there is evidence that the burrowing behavior of this species helps to maintain the low blood concentrations observed in the field. This could act in preventing water loss by evaporation and/or permitting absorption of water from the substrate in a way similar to that demonstrated by the brachyuran land crab, *Gecarcinus* (Bliss, 1956).

The osmotic concentration of urine on all three species was also determined.

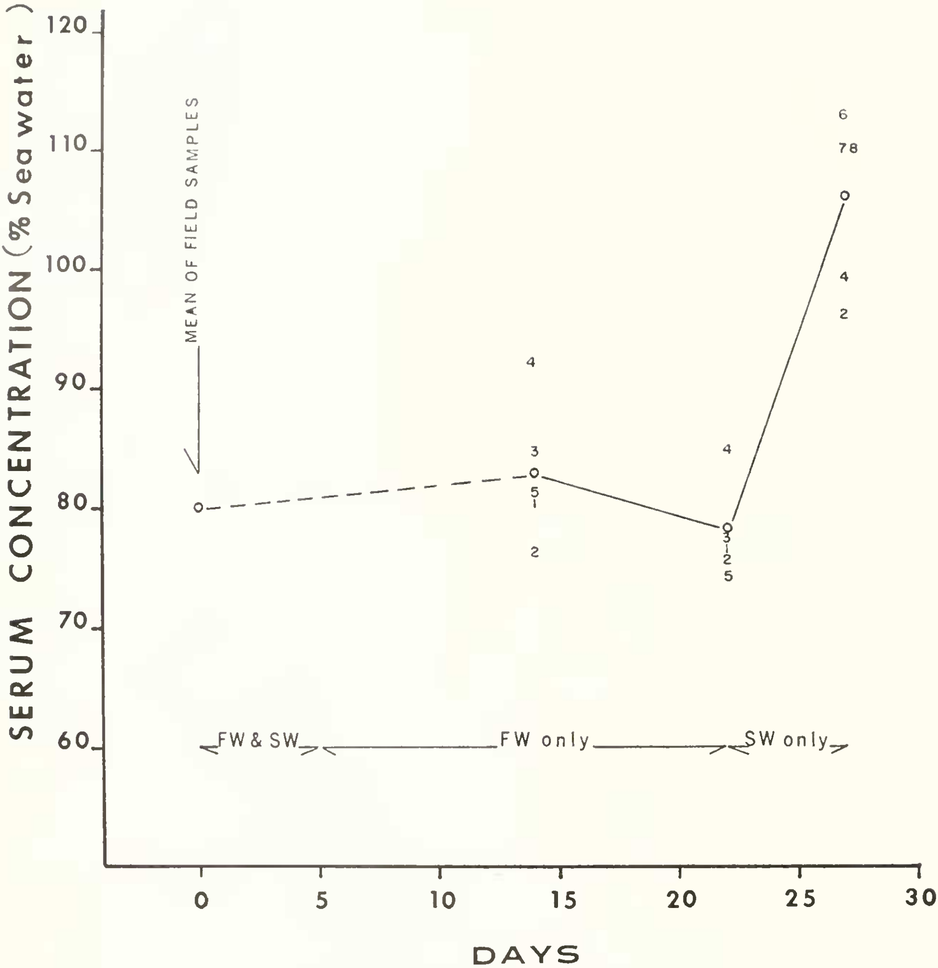

FIGURE 2. Response of *Coenobita brevimanus* to water of different salinity under laboratory conditions. Available water for different periods is indicated at the bottom of the graph. SW = normal sea water; FW = fresh water. Numerals represent individual specimens. Open circles represent mean values.

Thus, the ratio, urine concentration/blood concentration (u/s), for *C. perlatus* averaged unity for five specimens (range 0.98–1.02). One specimen had been exposed to both sea water and fresh water, for two days after capture. The other four specimens had been exposed to fresh water for two weeks. As seen by the range, the treatment made no difference. Four specimens of *C. brevimanus* exposed to fresh water for one to two weeks had a mean u/s value of 0.97 (range: 0.94–0.99). Attempts failed to extract urine from both species of *Coenobita* after they were exposed exclusively to sea water.

Only two u/s values were determined on individual specimens of *Birgus*. When

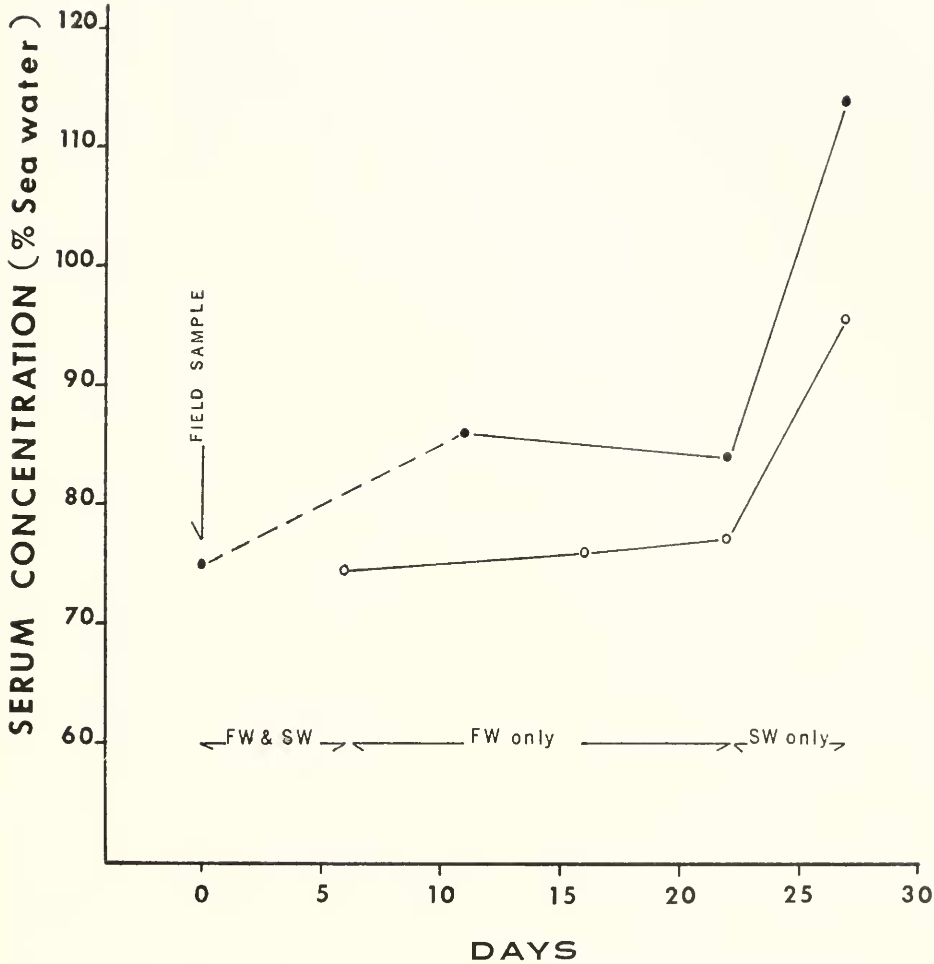

FIGURE 3. Response of two specimens of *Birgus* to water of different salinity under laboratory conditions. Line joining solid circles represents history of smaller crab. Line joining open circles represents history of larger crab. Available water for different periods is indicated at the bottom of the graph. SW = normal sea water; FW = fresh water.

one crab was exposed to sea water and fresh water for six days after capture, its u/s value was 0.95. The other specimen, which was exposed to the same conditions for only one day after capture, had a value of 0.82. However, urine samples from 5 crabs exposed to both sea water and fresh water for one day after capture averaged 66.7% sea water, which is less than the mean serum concentration for *Birgus* sampled in the field (74.7% sea water). There is a tendency, therefore, for the urine of both *C. brevimanus* and *Birgus* to be hypotonic to the blood. It is doubtful, however, that such a low degree of hypotonicity has any physiological significance. There thus is no evidence that the antennary glands of any of the three species are specially adaptive for terrestrial life. However, the small amounts of urine which could be extracted may indicate a low urine output, which would mean conservation of water. Loss of salt by way of the urine likely would present little problem to such a land animal inhabiting an environment exposed to sea spray.

Observations were made in the field on temperature and humidity. Thus, day-time relative humidities ranged between 60% and 80%; air temperatures about four feet above ground (including day and night) ranged between 25.0° and 33.2° C. and substrate temperatures between 26.0° and 28.5° in areas where crabs were captured. Body temperatures of *Birgus* captured in the daytime ranged between 26.7° and 30.0° C. There seemed, therefore, to be no critical stress imposed by these two physical factors on the land crabs of this area. Evaporation doubtless could occur from the body surface, especially if the crabs were exposed to the fresh tradewinds which blow constantly at this time of the year. However, the hermit crabs are protected from such evaporation by their adopted shells and *Birgus* is usually found in covered areas where it is shielded from the wind.

Discussion

Seurat (1904) reported that *Coenobita perlatus* in Mangareva habitually migrates to the sea at night to replenish its supply of water which it carries in its shell. Such a behavioral device might have initiated extended stays on land by the early terrestrial hermit crabs. The present investigation confirms that *C. perlatus* will fill its shell with sea water, but also that it will visit brackish water (58% sea water) for the same end. No standing fresh water could be found in the field during this investigation. However, Gross and Holland (1960) demonstrated that this species will enter fresh water in the laboratory, and this in turn effects a lower blood concentration than those observed in the present investigation. Thus, it is predicted that during the rainy season when there is an abundance of standing, fresh water, the average blood concentration of this species would be considerably lower. The large aggregation of *C. perlatus* found around a brackish pool as mentioned above cannot be interpreted as necessarily a preference for this salinity; rather it may reflect a preference for the calmness of the pool over the turbulence of the edge of the lagoon, where hermit crabs are tumbled violently by the lapping waves as they fill their shells.

It seems unlikely that any of the *C. brevimanus* sampled in the field depended on the sea for water. As shown in Figure 2 and Table II, exclusive access to sea water for 5 days elevates the blood concentration above anything observed in the field. Also, Table II shows that shell water of animals exposed to only sea water was much higher than that observed in the field animals.

Inasmuch as this species does not secrete large volumes of fluid into the shell, in the absence of surface water (Table II), the substantial quantities of shell water of low salinity observed in the field must have come from a source of fresh or brackish water which was not found within hundreds of meters of the site of capture. Now the shell water of 5 laboratory specimens of *C. brevimanus* averaged 60% sea water when only fresh water was available. Thus, the salinity of the shell water does not reveal the concentration of the water used by the crab, but it does indicate hypotonicity to sea water, however, and this excludes the sea as the sole source of water to the animal. Obviously, in the above case, the shell water concentration of 60% sea water indicates that body salts diffused into the shell. While the source of water for these animals in nature is uncertain, on one occasion a specimen of *C. brevimanus* was observed inside the shell of a rotten cocoanut which held fluid of an osmotic pressure equivalent to 35% sea water. Such a supply of water may be common in the wooded areas where both this species and *Birgus* could reach it as well as cocoanut milk.

Experiments in the laboratory demonstrated that *C. brevimanus* can fill its shell from a puddle which is only about 4 cm.^{2} in area and 1 cm. deep. Such a small source of water may have been common in the wooded areas but also would be easy for the investigator to have missed.

The evidence also suggests that *Birgus* does not depend on the sea for its source of water when it lives in the detritus of piles of rotten cocoanut. As shown in Figure 1, A, the blood concentration of such crabs was found to be greatly less than sea water, yet when *Birgus* is given access to only sea water, its blood elevates dramatically (Fig. 3). The source of water for *Birgus* on the dry, exposed islet of Jieroru seems more likely to be the sea water of the lagoon. The blood concentrations of all three specimens captured there were high. The soil was dry and, at the time the specimens were captured, unlikely to yield water to the body surface of the animals. There were no cocoanut trees and very little protection from the wind on the surface of the islet. The sparse vegetation was dry and exposed to sea spray, and thus unlikely to furnish adequate water if ingested. Still, these animals appeared normal and were very active. Harms (1932) reports that *Birgus* can obtain water from dew. This could be true in the wooded protected areas, such as found on Igurin and Giriinien Islets. It seems unlikely, however, that sufficient dew could condense on the windswept, exposed islet of Jieroru to supply *Birgus* with adequate water of low salinity. The serum concentrations of the animals sampled there attest to this. Dr. Edward Held (personal communication) has observed *Birgus* on the reef flat of Mui Islet at Eniwetok and captured two males whose tracks indicated they were returning from the reef flat to the wooded area. He has not observed *Birgus* at any time actually in sea water. It is reported that only females of adult *Birgus* re-enter the sea once they emerge, and then only to deposit their eggs (Harms, 1932). However, the cocoanut crab has been observed to drink sea water in captivity and was kept in an active condition exclusively on sea water for 78 days, after which time the blood osmotic concentration was equivalent to 118% sea water (Gross, 1955). This same investigation demonstrated that *Birgus* prefers fresh water to sea water, but will enter the latter occasionally if offered a choice between the two; the blood concentration of *Birgus* when given access to both fresh water and sea water was equivalent to about 90% sea water, which is considerably higher than the field samples taken in the wooded area of Igurin and Giriinien Islets during the present investigation. It is concluded that *Birgus* captured near cocoanut piles had sources of water of low salinity and did not depend on the sea for its water supply.

On the other hand, the only obvious reliable source of water for the Jieroru crabs during this drought period was the sea, and as shown above, this species can live for a sufficiently long period on sea water to survive the dry season. An alternative explanation for the high blood concentrations of the Jieroru crabs is that they were tolerating partial desiccation. It is possible that they could endure the dry season by such tolerance to desiccation but also by keeping water loss by evaporation at a minimum by sealing the entrances to their burrows; this was observed for two of the crabs captured on this dry islet.

The range of blood concentrations for *Birgus* and *C. brevimanus* captured on Giriinien and Igurin Islets is remarkably small compared to that of *C. perlatus*, which is not as discriminating in its choice of habitat as the other two species. The high degree of osmotic homeostasis observed in *Birgus* and *C. brevimanus* is effected by a behavioral rather than a physiological device, for the low blood concentrations cannot be maintained by either species in the absence of water of low salinity (Figs. 2 and 3). *C. perlatus* has demonstrated in the laboratory an ability to control its blood concentration by selectively entering sea water or fresh water (Gross and Holland, 1960). Yet this ability is not obvious in the field studies of this investigation. However, the paucity of fresh water or brackish water during the dry season probably precluded this behavioral activity. That is, tolerance to a wide range of blood osmotic concentrations by this species has permitted it to thrive in a variety of habitats, even though it probably is more selective when given the opportunity by the rainy season. Nevertheless, it is apparent that the dry season imposes no critical stress on the population of *C. perlatus*.

Birgus and *C. brevimanus* were usually confined to more specific environments than *C. perlatus*. Perhaps this precise discrimination is important in limiting the numbers of *C. brevimanus* and *Birgus* at Eniwetok, although both species show tolerance to considerable range of blood concentrations and *Birgus* on Jieroru Islet certainly demonstrated adaptability to stressed conditions.

Finally, it is suggested that the three subject species of this study represent three steps toward terrestrialness from the sea. *C. perlatus* seems closest to a marine existence because it habitually enters the sea to fill its adopted shell, a behavioral mechanism which was probably necessary for the initial step onto land by the hermit crabs; it prefers sea water to fresh water when offered a choice (Gross and Holland, 1960), and its high blood concentration in the field reflects an absence of fresh water which would be found only on land. Gibson-Hill (1947) considered that this species on Christmas Island is more strictly a marine animal which occasionally wanders away from the sea. *C. brevimanus* seems next closest to the sea. Although its blood concentration is dilute to sea water, it is more concentrated than that of *Birgus*. This species prefers fresh water to sea water when offered a choice, but it is still bound to an aquatic life by its adopted shell in which it carries a water supply of low salinity. *Birgus*, then, is most terrestrial, being independent of a gastropod shell, preferring fresh water to sea water and also having a blood concentration which is lowest of the three species when found in similar environmental situations.

Gross (1963b) has demonstrated that the terrestrial brachyuran crab, *Gecarcinus*, can tolerate sea water as its sole source of water only for about two weeks. This limited tolerance seems to be imposed by the inability of *Gecarcinus* to excrete salts. On the other hand, as mentioned above, *Birgus* can survive for at least 78 days on only sea water; yet after such treatment, its blood concentration (118% sea water), though higher than the available water, does not continue to elevate at the rate indicated in Figure 2. Rather, a plateau is reached at blood concentrations common to *C. perlatus* in nature, where the sea was its only source of water.

Thus, *Birgus*, which is probably the most terrestrial of the anomuran crabs, still seems closer to a marine existence or at least more tolerant of the sea than *Gecarcinus*, one of the most terrestrial of the brachyurans.

These studies were aided by a grant from the National Science Foundation, G-18978. The investigation at the Eniwetok Marine Biological Laboratory was supported financially by the U. S. Atomic Energy Commission. I wish to thank the following: Dr. Robert W. Hiatt for his role in making the Eniwetok trip possible; Dr. John S. Garth and Miss Janet Haig for kindly identifying *Coenobita brevimanus;* Dr. Edward Held for furnishing me unpublished information concerning the habits of *Birgus;* and Mr. Ronald Capen for his able technical assistance both in the field and in the laboratory.

Summary

1. Water balance in the anomuran crabs, *Birgus latro, Coenobita perlatus* and *Coenobita brevimanus*, was studied in the field at Eniwetok Atoll during the dry season.

2. *Birgus* and *C. brevimanus* usually are found in wooded areas in or near piles of rotten cocoanuts which are damp in their interiors. The osmotic concentration of the serum of *Birgus* and *C. brevimanus* from such conditions was relatively constant, averaging 74.7 and 80.3% sea water, respectively. Such animals do not depend on the sea for their source of water.

3. The osmotic concentration of serum from *Birgus* captured on the exposed, dry islet of Jieroru averaged 91.6% sea water. Evidence suggests that these animals were either using the sea as their source of water or were tolerating slow desiccation in well-sealed burrows.

4. *Coenobita perlatus* is more common and less discriminating than the other two species in its choice of habitat. It is found in such extremes as exposed positions at the edge of the lagoon and protected conditions, such as the interior of piles of cocoanuts in wooded areas.

5. Serum osmotic concentrations for *C. perlatus* taken in the field were usually hypertonic to the available sea water and ranged from 102% sea water (cocoanut piles) to 150% sea water (active at night in forest).

6. *Coenobita perlatus* was observed to enter sea water and brackish water at night; this resulted in filling their adopted shells with water.

7. Neither *Birgus* nor *C. brevimanus* was observed in sea water in nature, although both species will use sea water under laboratory conditions.

8. Shell water found in *C. brevimanus* taken from cocoanut piles was always hypotonic to sea water, but essentially isotonic to the serum. The source of shell water in this species was not found, but experiments demonstrated that such large volumes are not secreted.

9. *C. brevimanus* can thrive on a damp substrate in the absence of surface water for more than two weeks. The serum concentration following this treatment remains relatively low (mean: 86.4% sea water), but abnormal quantities of fresh water and sea water are used by the animal following treatment. This suggests that dehydration occurred and that salts also were lost to the damp substrate.

10. The osmotic concentration of urine in all three species is close to that of the blood, although it tends to be slightly hypotonic to the blood in *C. brevimanus* and *Birgus*. Therefore, there is no evidence that the antennary glands of these crabs are especially adaptive for terrestrial life.

11. Evidence presented suggests that the three subject species represent three steps from a marine life toward a terrestrial existence, *Birgus* being considered the most terrestrial and *C. perlatus* the closest to the sea.

12. *Birgus*, probably the most terrestrial of the anomuran crabs, is physiologically more marine in the adult stages than *Gecarcinus lateralis*, one of the most terrestrial brachyuran crabs.

LITERATURE CITED

Arnow, T., 1954. The hydrology of the northern Marshall Islands. Atoll Research Bulletin No. 30, issued by The Pacific Science Board, National Academy of Sciences, National Research Council.

Bliss, D. E., 1956. Neurosecretion and the control of growth in a decapod Crustacean. *In:* Bertil Hanström: Zoological Papers in Honour of His Sixty-fifth Birthday, November 20th, 1956, ed. K. G. Wingstrand. Lund, Sweden: Zoological Institute.

Edney, E. B., 1960. Terrestrial adaptations. *In:* The Physiology of Crustacea, ed. T. H. Waterman, Vol. 1, 367–393. New York: Academic Press.

Gibson-Hill, C. A., 1947. Field notes on the terrestrial crabs. *Bull. Raffles Mus.*, **18**: 43–52.

Gross, W. J., 1955. Aspects of osmotic regulation in crabs showing the terrestrial habit. *Amer. Nat.*, **89**: 205–222.

Gross, W. J., 1963a. Acclimation to hypersaline water in a crab. *Comp. Biochem. Physiol.*, **9**: 181–188.

Gross, W. J., 1963b. Cation and water balance in crabs showing the terrestrial habit. *Physiol. Zoöl.*, **36**: 312–324.

Gross, W. J., and P. Holland, 1960. Water and ionic regulation in a terrestrial hermit crab. *Physiol. Zoöl.*, **33**: 21–28.

Harms, J. W., 1932. Die Realisation von Genen und die consecutive Adaption. II. *Birgus latro* L., als Landkrebs und seine Beziehungen zu den Coenobiten. *Zeitschr. f. wiss. Zool.*, **140**: 167–290.

Pearse, A. S., 1934. Freezing points of bloods of certain littoral and estuarine animals. *Carnegie Inst. Washington Papers from Tortugas Laboratory*, **28**: 93–102.

Prosser, C. L., J. W. Green and T. S. Chow, 1955. Ionic and osmotic concentrations in blood and urine of *Pachygrapsus crassipes* acclimated to different salinities. *Biol. Bull.*, **109**: 99–107.

Seurat, L. G., 1904. Observations biologiques sur les Coénobites (*Coenobita perlata*, Edwards). *Bull. Muséum d'Histoire Naturelle*, **10**: 238–242.